I ON THE CICHLID FISHES OF THE GENUS *PELMATOCHROMIS* WITH PROPOSAL OF A NEW GENUS FOR *P. CONGICUS*; ON THE RELATIONSHIP BETWEEN *PELMATOCHROMIS* AND *TILAPIA* AND THE RECOGNITION OF *SAROTHERODON* AS A DISTINCT GENUS

AND

II A NEW SPECIES OF CICHLID FISHES OF RIVERS QUANZA AND BENGO, ANGOLA, WITH A LIST OF THE KNOWN CICHLIDAE OF THESE RIVERS AND A NOTE ON *PSEUDOCRENILABRUS NATALENSIS* FOWLER

BY

ETHELWYNN TREWAVAS

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ABSTRACT

Pelmatochromis nigrofasciatus Pellegrin is not, as has been suggested, a synonym of *P. ocellifer* Boulenger. The two species are defined and their relationships are discussed. The name *Pelmatochromis exsul* Trewavas was based on a misidentification of young *Hemichromis bimaculatus* Gill. Recognition of this fact removes the only record of *Pelmatochromis* from East Africa. A new genus is proposed for *P. congicus* Boulenger and a key to the species of *Pelmatochromis* is given. Reasons are given for excluding *Pelmatochromis* from *Tilapia* and retaining *T. busumana* in *Tilapia*. *Sarotherodon* Rüppell is considered to require full generic rank and *Tilapia* and *Sarotherodon* are defined.

Pelmatochromis Steindachner, 1895, type species *P. buettikoferi* Steindachner, by subsequent designation by Regan (1922), was restricted by Thys van den Audenaerde (1968a) to the species without a boot-shaped pad on the roof of the pharynx and with microbranchiospines on the outer sides of the second, third and fourth gill-arches, a restriction with which I agree.

Later, Thys (1968b) included *Pelmatochromis* in *Tilapia* and put *Tilapia busumana* (Günther, 1902) in the same subgenus. I dissent from both these opinions, and the present exercise arose from my examination in this context of *P. ocellifer* Boulenger, which Thys stated to have bicuspid teeth in the young. This, with the presence of a tilapia-mark on the dorsal fin in the same species, was his reason for including *Pelmatochromis* in *Tilapia*.

Dr M. Poll and Dr Thys kindly lent me some of the young '*P. ocellifer*' that had the bicuspid teeth and when, on comparing them with the only slightly bigger holotype of *P. ocellifer*, I told them that I thought they were not that species Dr Poll very kindly lent me a collection of specimens from the Museum at Tervuren that had been determined as *P. ocellifer*. They included two true *P. ocellifer* and 81 of the other species, which, as I now hope to show, is *P. nigrofasciatus* (Pellegrin), the types of which I examined in Paris some years ago, thanks to the kindness of the late Prof. Bertin.

With the holotype of *P. ocellifer* and the specimen figured by Boulenger (1915) we now have at Tervuren and BM(NH) four specimens of that species, respectively 63, 64·5, 85 and 100 mm in SL. In comparing characters showing allometry I use only specimens of the other species within this size-range, but for meristic characters I include also smaller and bigger fishes, up to SL 137 mm.

The two species have in common the following characters:

Scales 27–28 in the lateral line series, 14–16 around caudal peduncle; pattern of circuli in some scales roman, in others gothic (see p. 14 and fig. 10). Caudal peduncle very short, its length 0·5–0·8 of its depth. Depth of body 41·5–47·5% SL, length of head 35–39. Pectoral fin pointed or rounded, but not falcate, apparently complete in only two of the *P. ocellifer*, in which its length is 32·3–35·0% SL; in the other species it is 27·3–32·3%, shorter than head. Dorsal formula XIII 11–12, XIV 10–12 or XV 10–11, modal formula in *P. nigrofasciatus* XIV 11, modal total 26; a different formula in each of the four *P. ocellifer* (XIII 11, XIV 10–11, XV 11). Dorsal and anal soft rays produced in adult so that when they are laid back they reach a vertical in the posterior 2/3 of the caudal; pelvic ending in a long black filament extending to some part of the anal fin, in some as far as the hind end of its base; these prolongations occurring in both sexes. Caudal bluntly rounded, or truncate in the middle and rounded at the corners.

Except in interorbital width and length of premaxillary pedicels, proportions of parts of head alike in both species:- length of snout 29–36% length of head; diameter of eye 23–29; depth of preorbital 16·0–22·5, always smaller than eye; length of lower jaw 35–39.

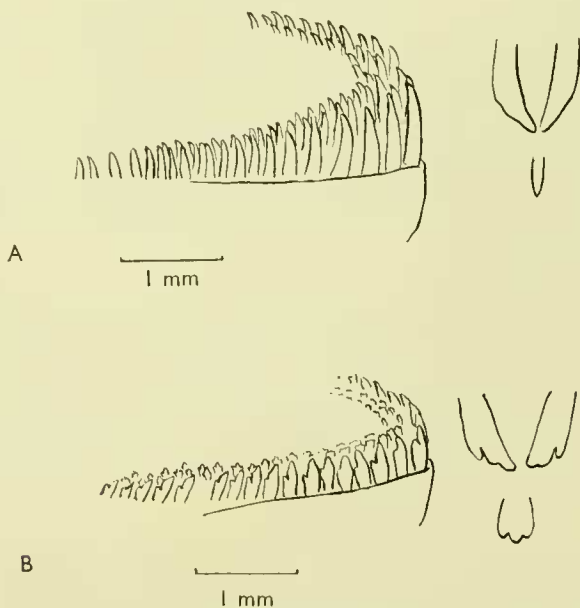Microbranchiospines present on outer sides of 2nd, 3rd, and 4th arches.

FIG. 1.   A.   Teeth of lower jaw in the holotype of *Pelmatochromis ocellifer*, SL 64 mm, and two outer and one inner teeth a little more enlarged.   B.   The same of *Tilapia ruweti* of SL 71 mm.

An intense opercular spot; a tilapia-mark on base of dorsal at junction of spinous and soft parts.

The distinguishing characters and synonymies are as follows.

P. ocellifer

Boulenger, 1899 : 104; id. 1901 : 421; id. 1915 : 391 fig. 264.
Paratilapia nigrofasciata (nec Pellegrin); Steindachner, 1914 : 54 (R. Ja).

HOLOTYPE.   BM(NH) 1898.7.9.16, 64·5 mm in SL, from Monsembe (Mosembe), Middle Congo, ca.1°20′ N, 19° E. coll. J. E. Weeks.

Teeth unicuspid, curved cones at all known stages, in bands 3–5 teeth wide in both jaws, 38–52 in outer series of upper jaw, about 6 anterior outer slightly longer than the rest, inner a little shorter than the outer (fig. 1A).

Premaxillary pedicels 27·7–30·1% length of head; interorbital width 30·1–33·2%.

Gill-rakers on first arch (2–3) + 1 + (6–7) (fig. 2).   Pad on roof of pharynx not boot-shaped, no groove or a very shallow one before it.   Width of lower pharyngeal bone 24·0–29·5% length of head; teeth of its middle rows few and spaced, some blunted (fig. 4).
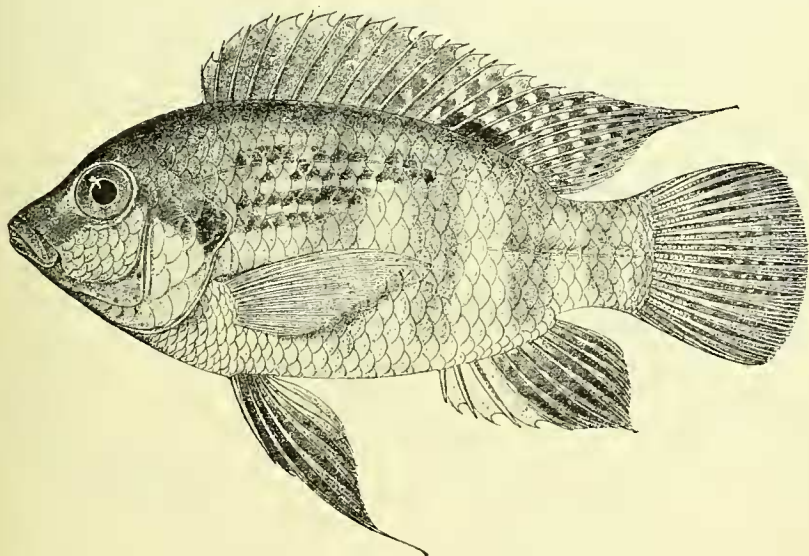
Pelmatochromis ocellifer.
Monsembe.

FIG. 2.   *Pelmatochromis ocellifer*, from Boulenger, 1915 fig. 264.

Series of scales on cheek 3–4; scales between origin of dorsal and lateral line 2½–3. Anal fin-rays III 7–8. Vertebrae 26 (3 specimens x-rayed).

In some specimens one or more dark horizontal streaks on anterior part of body, the uppermost above and on the upper lateral line, others uneven, below it (see fig. 2). Five broad dark vertical bars present or absent.

Known from three localities in the Congo basin—Monsembe on R. Congo, Karawa on a tributary of R. Mongala and R. Ja.

P. nigrofasciatus

Paratilapia nigrofasciata Pellegrin, 1900 : 353 (Nganchou, Congo, not far downstream from Kasai-Congo confluence).

Pelmatochromis nigrofasciatus (part.); Pellegrin, 1904 : 280, pl. vi fig. 2.

Pelmatochromis ocellifer (nec Boulenger); Steindachner, 1914 : 57 fig. 12 (R. Ja); Gosse, 1963 : 230; Thys van den Audenaerde, 1967 : 93; id. 1968a : fig. 13.

Paratilapia longipinnis Nichols & Griscom, 1917 : 728 fig. 29 (Congo at Coquilhatville and Irebu).

Teeth (fig. 4). In a young fish of SL 22 mm only one row of teeth is present in the lower jaw and some of these are notched, others have one cusp and a shoulder; there are only a few upper inner teeth, and these (and others when they develop) have one sharp cusp and a pair of shoulders; most of them retain this shape but from SL about 100 mm some of them are replaced by conical teeth. Already at SL 38 mm there are no more notched teeth in the outer series, but the teeth are still flattened in section and shouldered; later the shoulder is lost and more and more of the outer teeth become conical. The last to retain a shoulder are the lateral teeth of the lower jaw, where the band may be a little wider and the teeth overlap obliquely; in large specimens these too become conical.

The outer teeth are more numerous and close-set than in *P. ocellifer*, 54–64 in the upper jaw, 74 in a specimen of SL 116 mm. There are 4 rows in the upper jaw,
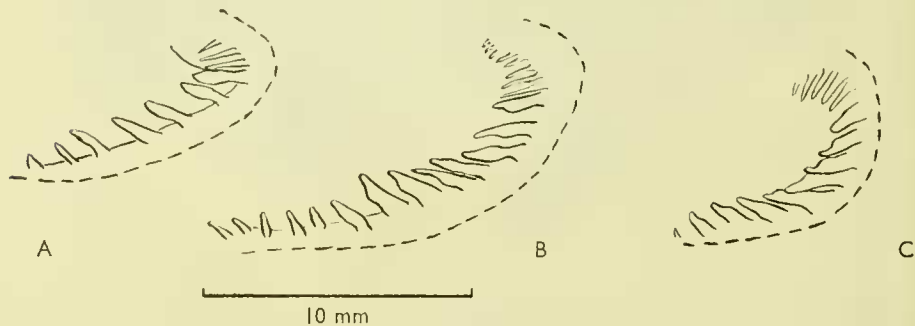

FIG. 3. Outer gill-rakers of first arch in, A, *Pelmatochromis ocellifer* of SL 100 mm, B and C, *P. nigrofasciatus* of 109 and 61 mm respectively.

3 in the lower, unevenly broadening to an extra row in both jaws in large specimens, and the inner are much smaller than the outer.

Premaxillary pedicels 21·6–26·8% length of head (27·7 in one), interorbital width 33·5–38·0.

Gill-rakers on first arch (4–8) + 1 + (8–14), the upper very slender (fig. 3). Pad on roof of pharynx moderate, a shallow groove in front of it.

Lower pharyngeal bone slender, with all the teeth very slender, up to twice as many in a middle row as in a comparable specimen of *P. ocellifer* (fig. 5). In a young fish of SL 61 mm there is a total of about 135 teeth on the bone as compared with 120 in a 64·5 mm *P. ocellifer* and 110 in the 100 mm specimen of that species.

Scales of cheek in 3 rows, between origin of dorsal and lateral line $3\frac{1}{2}$–4. Anal III 9–10. Vertebrae 26 (f.4) or 27 (f.1); in the last, one vertebra has an abnormally short centrum.

A scaly sheath at base of anal fin. Rows of small scales along the caudal rays for $\frac{1}{4}$ to $\frac{1}{2}$ of their length.

Colour in alcohol: Six dark vertical bands of varying intensity on the body, the first immediately behind operculum, the last at the ene of caudal peduncle, these bearing up to six large, round blotches in series from behind opercular spot to end of caudal peduncle; of ten a faint or incomplete upper band or series of blotches. In a few specimens upper end of transverse band immediately below the tilapia-mark intensified, suggesting a "pelmatochromis-mark" like that characteristic of *P. buettikoferi*. Tilapia-mark becoming smaller in adult and finally vanishing or obscured by general dark colour of fin. Some individuals with alternate dark and clear spots on caudal and soft dorsal and a white upper edge to dorsal fin.
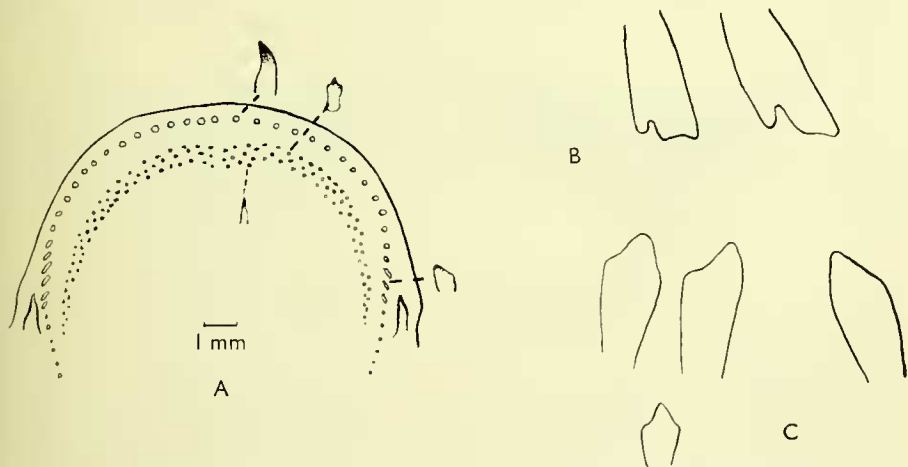

Fig. 4. *P. nigrofasciatus.* A. Plan of dentition of lower jaw in a fish of SL 120 mm. B. Two outer teeth of a juvenile of SL 22 mm. C. Three outer and one inner teeth of a juvenile of SL 35 mm.

Colour in life: In the young male described by Matthes (1964) the vertical bands and blotches were present but rather faint, the upper edge of the dorsal was yellow and series of spots were black on the anterior part of the fin, red on the posterior rays. The anal bore black spots proximally, red distally on a yellow ground. The outer rays of the pelvics were black, inner yellow. Filamentous tips of dorsal, anal and pelvics were black.

The diet (Matthes, l.c.) is predominantly vegetable, the stomachs of the two specimens examined by Matthes containing masses of filamentous and unicellular algae as well as insect remains and mud.

Reproduction. Gosse records that it is a substrate-spawner and guarder of the brood.

Natural distribution: throughout the central Congo basin from Yangambi to Kinshassa, including R. Rubi, R. Chuapa, R. Ja and the Kasai.

Pellegrin's description of the types is in agreement with this rather than with *P. ocellifer* in the following details:- gill rakers "une dixaine a la partie inferieure au premier arc branchial"; 9 soft rays in the anal fin; six broad transverse bands on the body; teeth small and "peu distinctes", the outer a little longer than the inner. All these details are confirmed by my notes on the types, in which I found 9 gill-rakers on the lower part of the arch, excluding one at the joint.

Steindachner evidently had both species but transposed their names, calling the one with the narrower interorbital and 8 gill-rakers *P. nigrofasciatus*, the one with the wider interorbital and five dark spots of unequal sizes on the flank *P. ocellifer*. He described under *P. ocellifer* a dentition perfectly corresponding to that found in *P. nigrofasciatus* described above, including the broadening of the lower band near the corner of the mouth. The inner teeth are described as "winzig" and the outer as not insignificantly b'gger than the inner. A discrepancy is the ascription of 5 rows of cheek scales to this species, but his figure shows only three and is a recognizable *P. nigrofasciatus*.

This is the only record of the species in R. Ja, a secondary tributary of the Congo.

Pellegrin (1931 : 211) and Daget (1961 : 585) record *P. nigrofasciatus* from the Niari-Kouilou and we have one at the BM (NH) collected by M Ch.Roux near Point Noir. They are more slender (depth 33–40% SL) but otherwise agree with the Congo specimens.

THE STATUS OF *PELMATOCHROMIS EXSUL*

Having corrected a misidentification of Dr Poll's, I have now to correct a more serious one of my own.

Pelmatochromis exsul Trewavas: (1933 p. 320, fig. 4) was described from 3 small specimens, 25·5+6·5 to 34·5+10 mm long, from Lake Rudolf. On re-examining them I have come to the conclusion that they are young *Hemichromis bimaculatus* Gill, 1863. Unlike all our preserved specimens they have no distinct black spot on the flank. I have looked at the base of the skull in one and find that its apophysis for the upper pharyngeal bones is so little developed that it could hardly be used for diagnosis, but it might well be of the *Hemichromis* type. Numbers of scales,

finrays and gill-rakers are in agreement with *H. bimaculatus* and the arrangement of the circuli of the scales is gothic (see p. 14 and fig. 10).

This species occurs in the Nile, whence the fish-fauna of Lake Rudolf is derived, and although it has not been caught in subsequent collections from the lake it is probably there in suitable habitats.

This correction removes an apparent anomaly in the distribution of *Pelmatochromis*.
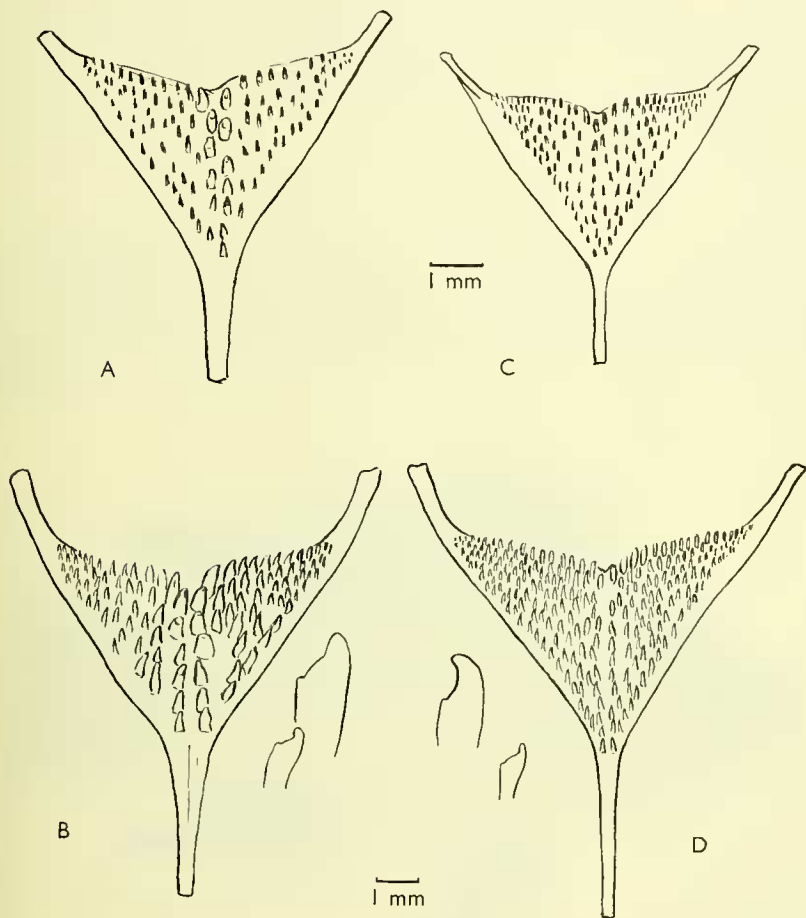

FIG. 5. Lower pharyngeal bones of *Pelmatochromis ocellifer*, A, at SL 64 mm, B, SL 100 mm; and *P. nigrofasciatus*, C, at SL 61 mm and D, SL 116 mm. A middle posterior tooth and an anterolateral are shown enlarged for each of the adult fishes.

INTERRELATIONSHIPS OF THE SPECIES OF *PELMATOCHROMIS*

It is to *P. nigrofasciatus* and not *P. ocellifer* that Thys is referring when he writes (1968a) that *P. congicus* is a specialized form derived from *P. ocellifer*. With the substitution of the name I would agree with this opinion, but the specialization has gone so far that *P. congicus* is best considered as a separate genus.

P. ocellifer and *P. buettikoferi* are alike in the dentition of jaws and pharynx in which they contrast with *P. nigrofasciatus*, especially developmentally. On the other hand *P. buettikoferi* differs from both Congo species in the colour-pattern, having no tilapia-mark, but instead a dark spot on the back below the site of the tilapia-mark of others, and its pelvic, dorsal and anal fins are less produced. *P. ocellifer* has a shorter series of epibranchial gill-rakers on the first arch than either of the other two species. Some other aspects of their structure will be considered in discussing their alleged relationship with *Tilapia*.

I propose a new genus, *Pterochromis*, for the type species *P. congicus* Boulenger, distinguished from *Pelmatochromis* by its large oblique mouth, long slender gill-rakers and more specialized dentition. The two genera have in common the following features :-

Apophysis for the upper pharyngeals formed by the parasphenoid alone; all teeth unicuspid in adult; pad on roof of pharynx sessile; microbranchiospines present; lateral lines overlapping by only one or two scales if at all, the upper separated from the dorsum posteriorly by $1\frac{1}{2}$ scales; scales cycloid, partly roman, partly gothic (see fig. 10).; vertebrae 26 or 27, mode 26; scales 27 or 28 in lateral line series.
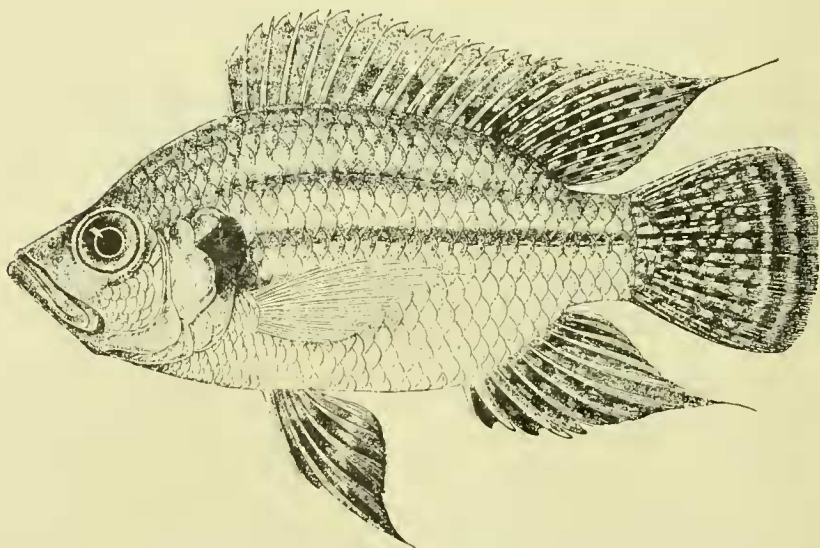
They are distinguished from each other as follows :-

FIG. 6.   *Pterochromis congicus* from Boulenger, 1915 fig. 261.

PELMATOCHROMIS Steindachner

Lower jaw 35–42% length of head, premaxillary pedicels $21\frac{1}{2}$–33%; mouth at an angle of 20–40° with the horizontal; gill-rakers (2–8) + 1 + (6–14) on first arch. Three species, *P. buettikoferi*, *P. ocellifer*, *P. nigrofasciatus*.

PTEROCHROMIS n. gen.

Type *Pelmatochromis congicus* Boulenger = *Pterochromis congicus*.

Lower jaw 51–$54\frac{1}{2}$% length of head, premaxillary pedicels 42–$43\frac{1}{2}$%; mouth at an angle of 40–50° with the horizontal; gill-rakers (9–11) + 1 + (17–19) on first arch (fig. 3).

A single species.

Pterochromis congicus

Pelmatochromis congicus Boulenger, 1897 : 422 (Stanley Falls); id. 1898 : 149; id. 1901 : 437 (Stanley Falls and L. Obéké); Pellegrin, 1904 : 287; Boulenger, 1915 : 386, fig. 261; Thys van den Audenaerde, 1968a : 371, fig. 14 (after Boulenger).

The measurements in the generic definition have been taken from 5 specimens of SL 58–152 mm including the holotype, a specimen from L. Obéké and 3 from R. Momboyo.
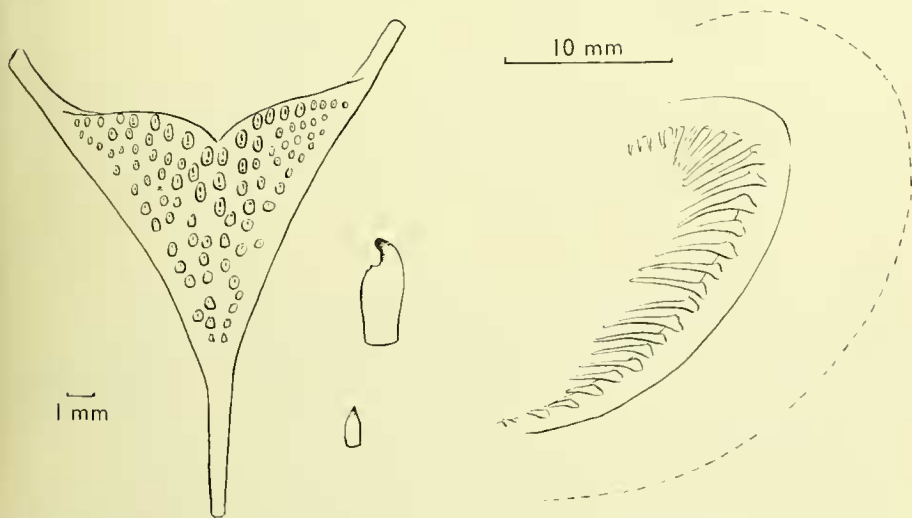

Fig. 7. *Pterochromis congicus*, lower pharyngeal bone with isolated posterior and anterior teeth; and rakers of first gill-arch in a specimen of SL 150 mm.

Dentition.   In the 68 mm specimen all the teeth are unicuspid with no shoulder. In the 68 and 71 mm specimens there is only one, irregular inner row, of few, very small teeth; in the 71 mm fish I cannot find any inner teeth in the upper jaw.   At SL 150 mm there are 1–2 irregular rows of inner teeth in the upper jaw, 2 in the lower. In all the outer teeth are conical, firm, the two or three anterior on each side in the lower jaw spaced and thicker than the rest.   In the 150 mm fish the tooth-band of the lower jaw is broadened anteriorly by wider spacing between the rows (fig. 8).

There is no evidence of a pluricuspid stage.   Both this species and *Pelmatochromis nigrofasciatus* have a characteristically pigmented tooth-bed in which each inner tooth pierces a tiny pigment-free disc.

The pharyngeal teeth are narrow but rather coarse, the posterior bicuspid, the anterior conical. (fig. 7).
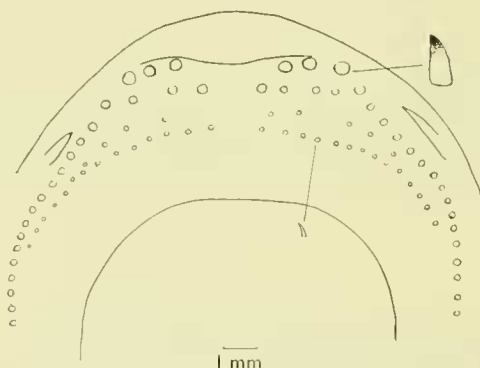

FIG. 8.   *Pterochromis congicus*, SL 150 mm, plan of dentition of lower jaw and isolated outer and inner teeth to the same scale.

KEY TO THE SPECIES OF *PELMATOCHROMIS*

1a   Outer teeth unicuspid in adult, shouldered in juveniles, some notched in very young; inner much smaller than outer, some retaining minor cusps in adult, others replaced by unicuspids; premaxillary pedicels 21·5–27·7% length of head; gill-rakers 8–14 on lower part of first arch; a tilapia mark.   Congo   .   ***nigrofasciatus***

1b   Teeth unicuspid, curved cones at all known stages, inner shaped as outer and only a little smaller; premaxillary pedicels 27·7–33·0% length of head; gill-rakers 6–8 on lower part of first arch   .   .   .   .   2.

2a   A tilapia-mark; lower jaw 35–38% length of head; 2 or 3 epibranchial gill-rakers. Congo   .   .   .   .   ***ocellifer***

2b   No tilapia-mark in adult, but a black spot on the back below junction of spinous and soft dorsal; lower jaw 38–42% length of head; 3–6 epibranchial gill-rakers.   Liberia to Sierra Leone   .   .   .   .   ***buettikoferi***

THE RELATIONSHIP BETWEEN *PELMATOCHROMIS* AND *TILAPIA*

To include as Thys (1968b : xxvii–xxix) does *Pelmatochromis buettikoferi*, *P. ocellifer*, *P. nigrofasciatus*, *Pt. congicus* and *Tilapia busumana* in the same subgenus requires a definition full of alternatives. I will proceed to examine the characters on which he relies and some others that seem to me to be relevant to the relationship.

Dentition of jaws

We have no *P. ocellifer* smaller than 63 mm SL and in this the teeth are unisucpid, curved cones of the adult type. The same is true of the smallest *P. buettikoferi* examined, a specimen of 28 mm SL. The teeth of *P. nigrofasciatus* from SL 22 mm to the adult have been described on p. 6 and fig. 4.

The only species of *Tilapia* in which the very early development of the teeth has been described is *T. tholloni*. Fishelson (1966 : 197) states that they are unicuspid at first appearance, but at the 15th day after fertilization there are already tricuspid teeth. In his fig. 23 of a 16-day larva one minor cusp is visible on each clearly defined tooth. This goes on to develop into the well-known *Tilapia* dentition, with bicuspid outer and tricuspid inner teeth.
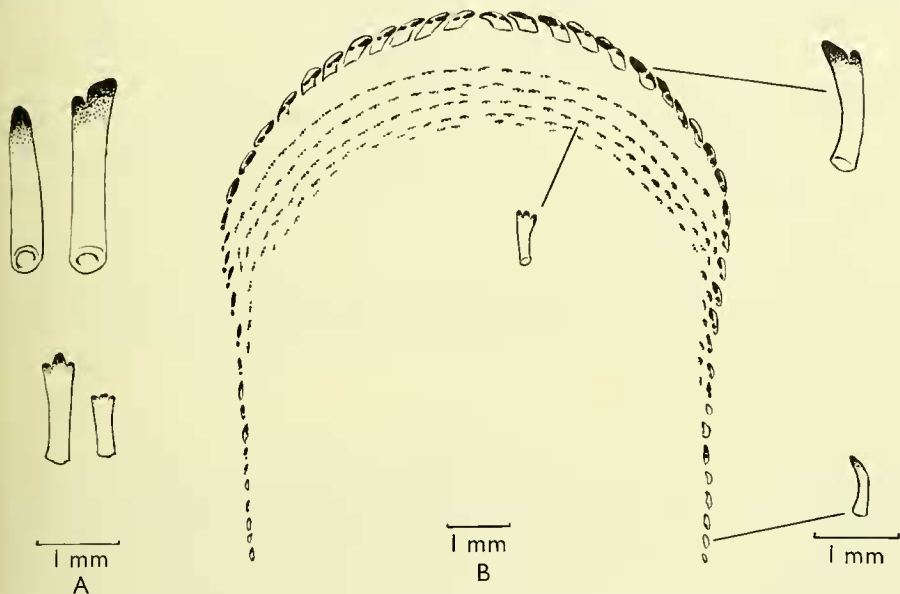
FIG. 9.   *Tilapia busumana*, A, isolated teeth from a specimen of SL 156 mm; above, one of the 22 outer lateral simple teeth from right ramus of upper jaw and one of the 11 bicuspid anterior outer teeth from the same; below, inner teeth from respectively the row next to the bicuspids and the inmost row; the open lower ends of the outer teeth are seen because of the curve of the axis of each in a plane at right angles to the page. B, dentition of lower jaw, with enlarged drawings of three of the teeth in a fish of SL 111 mm.

C

In *T. busumana*, where in the advanced adult progressively more of the lateral teeth become replaced by strong unicuspids, the anterior retain a minor cusp and the inner, at first with three subequal cusps, retain two reduced minor cusps (fig. 9). Up to SL 110–120 mm there is a typical *Tilapia*-dentition of bi- and tricispid teeth, the inner still with three subequal cusps and only 7 or 8 unicuspids at the ends of the outer row of the upper jaw.

In the Zambezi populations of *Tilapia ruweti* (Poll & Thys) some of the teeth become pointed in adults by reduction in the anterior or suppression in the posterior teeth of the minor cusps.

The food of these two species of *Tilapia* has not been fully studied, but by analogy it may be supposed that the teeth of *T. ruweti* become adapted to seizing small invertebrates, which perhaps form an increasing part of the diet as the fish grows. The lateral unicuspids of *T. busumana* are in the wrong position for seizing and are more likely to act as a barrier to prevent loss of food items taken in at the front of the mouth (c.f. the dentition of *Pseudotropheus, Tropheus* and *Simochromis* of Lakes Malawi and Tankanyika).

Thus we have four types of dentition in the species under consideration :-

(1) Outer and inner teeth curved, conical at all stages (from SL 28 mm). **P. buettikoferi, P. ocellifer.** (and *Pterochromis*)

(2) Outer teeth notched or shouldered in the very young, then shouldered, then conical; inner shouldered, then mixed shouldered and conical, then conical, much smaller than outer. **P. nigrofasciatus.**

(3) Teeth pluricuspid at first, becoming pointed in adult by reduction or, in some teeth, suppression of the minor cusps. Some individuals of **Tilapia ruweti.**

(4) Outer teeth bicuspid, the lateral replaced in large individuals by strong conical teeth; inner tricuspid, the lateral cusps reduced in fishes of 130 mm or more. **T. busumana.**

The differences, examined closely, are such as to need overwhelming support from other characters before either species of *Tilapia* in united in one subgenus with *Pelmatochromis*, and the position of *P. nigrofasciatus* in relation to both genera requires scrutiny.

Scales

In African Cichlidae there is considerable diversity in the structure of the scales. Leaving out of consideration the ctenoid scales of the *Haplochromis* group, there are in West Africa two main types of cycloid scales based on the arrangement of the circuli. I name them by analogy with architectural arches roman and gothic. In roman scales the circuli in the posterior field are parallel to the edge, in gothic they meet at an angle (fig. 10). All the scales are gothic in *Hemichromis* and in "*Pelmatochromis*" *thomasi* Boulenger (not a true *Pelmatochromis*). *Pelmatochromis buettikoferi, P. ocellifer, P. nigrofasciatus and Pt. congicus* all have a mixture of gothic and roman, except in adult *Pt. congicus*, where all are roman. In *T. busumana* and all the species of *Tilapia* except *T. ruweti* (Poll and Thys) all the scales are roman. In both *Pelmatochromis* and *Tilapia* a large part of the posterior field of many of the

scales may become granular, so that the circuli are partly obliterated, but it is generally possible to see the direction of the circuli from the other part of the scale. *Tilapia ruweti* is one of the species having a granular area in many scales; where the circuli are complete they are either roman or gothic, in the latter case the angle at which the circuli meet is blunt, represented by a narrow curve.

Vertebrae (Table I.)

In African Cichlidae it may be accepted that low numbers of vertebrae are primitive except where numbers are secondarily reduced in waters of high temperature. In the three species of *Pelmatochromis* taken collectively the modal number is 26. The only *Tilapia* having the same mode is *T. guinasana*, which Thys has placed in a separate subgenus* on account of its large scales. *T. busumana* agrees with the type-species of *Tilapia* in having a strong mode at 27. In *T. zillii* (and other species of the subgenus *Coptodon* except *T. rendalli*) the mode is 28.

Parenthetically, the three specimens of *P. buettikoferi* with 26 vertebrae are from Liberia, near the type-locality, the three with 27 from Sierra Leone and R. Corbal, the latter the type of *P. corbali* Boulenger, regarded as a synonym. Only more data can determine the significance, if any, of this.

TABLE I.   Frequencies of vertebral numbers in
Pelmatochromis, Pterochromis and species of *Tilapia*

Number of vertebrae	26	27	28	29
Pelmatochromis				
P. ocellifer	3			
P. buettikoferi	3	3		
P. nigrofasciatus	4	1		
Pterochromis				
P. congicus	2			
Tilapia				
T. ruweti		3		
T. sparrmanii	1	10	5	
T. busumana	1	25	2	
T. guinasana	11			
T. zillii		5	33	2

The tilapia-mark

The tilapia-mark, a black spot, often surrounded by a transparent or yellow ring, at the junction of spinous and soft parts of the dorsal fin, is, as its name indicates, very characteristic of the species of *Tilapia* and *Sarotherodon***; either throughout life or in juveniles. But it turns up too in other, related genera, derivatives as I interpret it of the source-group of *Tilapia*. Among these it is more sporadic than in *Tilapia* or *Sarotherodon*. So, in *Pelmatochromis* it is present in *P. ocellifer*, absent in *P. buettikoferi*. *P. nigrofasciatus* and *Pt. congicus* have a tilapia-mark in the young and this becomes drawn out in a direction parallel to the fin-rays and then

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* The name *Trewavasia* proposed for this subgenus by Thys is preoccupied.
** Until now considered a subgenus of *Tilapia*. I consider it worthy of generic rank. See p. 20.

disappears in the adult. In young *Chromidotilapia* sp. of West Cameroon there is a similar mark and the females of *C. batesii* have a more vaguely defined mark in the same position. In *Stomatepia mariae* of Barombi Mbo, a species with a predacious habit and aspect, there is a typical tilapia-mark in the young, becoming elongate and drawn out parallel to the rays in the adult and finally vanishing. On the other hand, of two sibling species of *Sarotherodon* in Barombi Mbo, one has a conspicuous tilapia-mark in the young, the other has none. Young of *Leptotilapia irvinei* have a tilapia-mark (Roman, 1966).

In short, the presence or absence of a tilapia-mark is not absolutely diagnostic of these genera, although it must be taken into account in assessing relationships.

A colour feature in *T. busumana*

The postero-dorsal corner of the caudal and the tip of the soft dorsal in *T. busumana* are narrowly margined with white or red according to the environment. Although this is a common pattern in *Chromidotilapia* (and *Pelvicachromis* Thys), *T. busumana* is not the only *Tilapia* exhibiting it. It is found too in *T. louka* Thys and *T. mariae* Boulenger.

Length of intestine

In a *P. buettikoferi* of 74 mm SL the intestine is about 2·3 times the SL, in a *T. busumana* of 76 mm it is 2·5 times this length. This is short for *Tilapia* and is
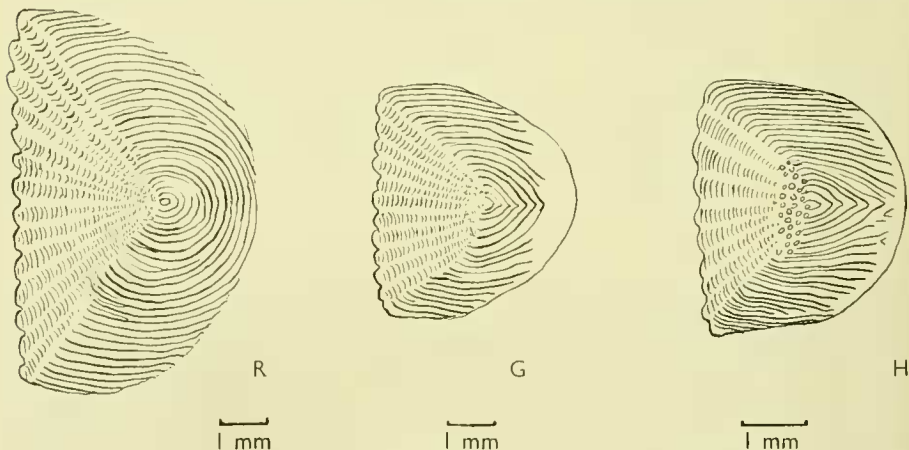

Fig. 10. Scales from between the anal fin and the lateral line in R, *Tilapia busumana* (roman) and, G, *Pelmatochromis buettikoferi* (gothic). In *T. busumana* the circuli are more numerous and close-set than in the drawing. For comparison, H, a flank scale of *Hemichromis bimaculatus* (gothic).

in line with the changed dentition and presumably diet in adult *T. busumana*. It is a feature in which this species resembles *Pelmatochromis* more than other species of *Tilapia*.

The epibranchial structures

Glandular and sensory pads on the roof of the pharynx are present in most (all?) cichlids anterolaterally to the upper pharyngeal teeth.

When Steindachner proposed the subgenus *Pelmatochromis* (Gr. pelma, gen. pelmato = the sole of the foot, referring to the shape of the pad) he included two species, *P. buettikoferi* and *P. jentinki*, without designating either as type. Regan (1922) used the criterion of page priority to designate *P. buettikoferi* as type-species, and this is the one in which the pad is not boot-shaped, as Steindachner knew. Pellegrin, Boulenger and Regan eventually considered *Pelmatochromis* to include also *Chromidotilapia* Boulenger, 1898 (type *C. kingsleyae*), finding a gradation between the extreme shapes of the pad. Thys (1968a) has revalidated *Chromidotilapia* for species with a boot-shaped pad, since in this group its presence or absence is correlated with the respective absence and presence of microbranchiospines. This seems to be a natural division, although that the correlation is not always functionally or genetically necessary is shown by the fact that *Tylochromis* and *Callochromis*, for instance, have both a boot-shaped pad and microbranchiospines.

Thys stated (1968a : 374) that the projecting pad is a glandular sac with an opening on each side in front of the upper pharyngeal tooth patches. This I
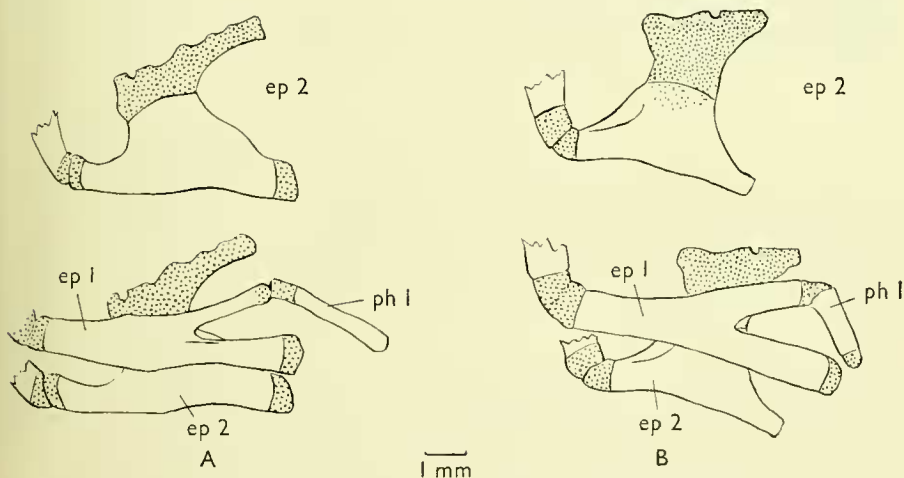

Fig. 11. Upper bones of 1st and 2nd branchial arches in, A, *Tilapia busumana*, B, *Pelmatochromis nigrofasciatus*. The bones are drawn as if detached from the skull and viewed from above. Cartilage dotted. *ep* 1, *ep* 2, 1st and 2nd epibranchial; *ph* 1, 1st pharyngobranchial. The 2nd pharyngobranchial, a small toothed bone, is not shown.

cannot confirm by examination with a dissecting microscope for either the boot-shaped or the sessile pad, and Thys gave no evidence for his statement. Dissection of both the hanging and the sessile pads reveals only connective tissue inside, often fat-laden. In the midst of this is a lamina of cartilage and bone that is an expansion of the anterior edge of the second epibranchial (fig. 11). On the oral side the membrane is raised into ridges and bosses bearing sensory cells. The histology of these pads has been little studied. Al Hussaini & Kholy (1954) found in the pharynx of *Tilapia nilotica* columnar cells interspersed with granular cells. Stolk (1957) described secretory cells in the pads of female *Haplochrmis multicolor* without comparing them with the males. Fishelson (1956 : 588, fig. 19) demonstrated both glandular and sensory cells in *Tilapia tholloni* not only between and beside the upper pharygeal tooth-plates, but also on the floor of the pharynx, including the gill-arches.

Macroscopically the pad is very similar in *Pelmatochromis* and *Tilapia*, but between *Tilapia* on the one hand and two of the species of *Pelmatochromis* (and *Pt. congicus*) on the other there is a difference in the epibranchial structures. In these (*P. buettikoferi* and *P. nigrofasciatus*) as also in *Chromidotilapia*, there is a long series of slender epibranchial gill-rakers on the first arch and the fold of skin (frenum) at the hinge between suspensorium and epibranchial is remote from the epi-ceratobranchial joint. This leaves a free passage for a current, respiratory or food-bearing, to pass between the pharynx and the upper part of the parabranchial chamber, in which direction can only be tested by experiment (fig. 12A).

In *Tilapia*, on the other hand, the epibranchial gill-rakers are few, short and blunt and the frenum is attached near the epi-ceratobranchial joint. The upper gill-filaments are attached along a line turning inwards behind the frenum, which would obstruct any flow of water between the upper filaments and the pharynx (fig. 12B).
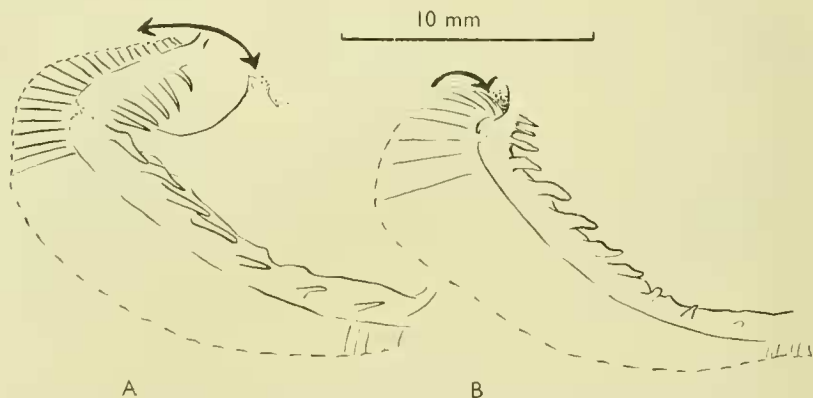

FIG. 12. Outer gill-rakers of first arch in, A, *Pelmatochromis buettikoferi* of SL 98 mm, B, *Tilapia busumana* of SL 91 mm. The arrows show possible directions of the current in the upper part of the gill-chamber.

P. buettikoferi and *P. nigrofasciatus* have a transverse groove on the roof of the pharynx between the top of the first epibranchial and the middle of the pharyngeal roof.   This is less sharply demarcated than a similar groove in the cichlids with the hanging pad, but the groove and the free epibranchial passage must together influence the currents at the back of the pharynx, which can hardly be the same as those of *Tilapia* and other genera with an obstructing frenum and no transverse groove.

Pelmatochromis ocellifer, in the few, rather damaged specimens at our disposal, seems to have an epibranchial region more like that of *Tilapia* than the other species of *Pelmatochromis*, although in other respects it resembles the latter.

CONCLUSIONS ON *PELMATOCHROMIS* AND *TILAPIA*

The only species of *Pelmatochromis* showing any evidence of derivation from an ancestor with a *Tilapia*-like dentition is *P. nigrofasciatus*.   The fact that the outer teeth are notched only at such an early stage that they can hardly be functional as such suggests that they are a vestigial feature derived from an ancestor that had indeed a *Tilapia*-like dentition.   That the ancestor was a *Tilapia* may be doubted because of the epibranchial structures and there is no evidence at all of such an ancestral dentition for *P. buettikoferi* and *P. ocellifer*.   The adult dentition of *P. nigrofasciatus* is itself so distinct as to suggest that *Pelmatochromis* is diphyletic. If this is so, it will not, in my opinion, be mended by putting *P. nigrofasciatus* in *Tilapia*, although the two (?) ancestral species of *Pelmatochromis* and the one (?) of *Tilapia* must have been rather closely related.   Any opinion as to whether *Tilapia* and *P. nigrofasciatus* can be traced back to a single ancestor that was already separate from the ancestor of *P. buettikoferi* and *P. ocellifer* must be purely speculative.   The creation of a separate genus for *P. nigrofasciatus* would express both our guesses and our doubts, but the purpose of genera is not solely to express the speculations of taxonomists (although we endeavour not to allow them to cut across the more firmly based of these) and I propose to leave *P. nigrofasciatus* in *Pelmatochromis* with the above qualifications.

On both geographical and structural grounds the *Tilapia* coming nearest to *P. nigrofasciatus* is *T. ruweti*, of swampy pools and streams on either side of the Congo-Zambezi water-shed.   It was originally described as a *Pelmatochromis* because of its rounded caudal and its spotted, showy vertical fins.   This, however, is *Tilapia*-like in its few (2–3, usually 2) short epibranchial gill-rakers, 27 vertebrae and its dentition and it so closely resembles *Tilapia sparrmanii* as to be difficult to distinguish from it even in life.

As for *T. busumana*, this has a functional *Tilapia*-dentition far into adult life and the replacement of its lateral teeth by unicuspids is probably not a strictly parallel event to the development of the adult dentition of *P. nigrofasciatus*.   Functionally it cannot serve the same purpose (p. 14).   A more exact parallel is found in the transformation that occurs in adult males of *Sarotherodon angolensis* Trewavas (p.29 below).   The relationship of *T. busumana* with its geographical neighbour *P. buettikoferi* is not very close, perhaps at the subfamilial level, although other genera must be taken into account (including the South American) before subfamilies can be established with confidence within the Cichlidae.

STATUS AND DEFINITION OF *TILAPIA* AND *SAROTHERODON*

During recent years information has been accumulating on the species of *Tilapia* in the broad sense to show that on both structural and behavioural features they fall into two well-defined groups. Thys van den Audenaerde (1968) has indeed recognised three "Sections", but the first two fall together on their reproductive pattern and the structures associated with it. The earliest name of the genus-group for the species of Thys's sections I and II is *Tilapia* A. Smith, 1840, for his section III *Sarotherodon* Rüppell, 1853. In 1968 Thys left the latter as a subgenus of *Tilapia* (as it was used by Regan in 1920 and Trewavas in 1966), but in 1970 (p. 295) he writes of *Coptodon* Gervais (while listing it as a subgenus of *Tilapia*) that it and *Sarotherodon* are "major subgenera, in fact good genera". In 1971 he again uses it as a subgenus.

I cannot find any good reason for regarding *Coptodon* as more than subgenerically distinct from *Tilapia*, but if Thys means to say that *Tilapia* and *Sarotherodon* are to be regarded as genera I would agree with him and have now adopted this usage (Trewavas, Green and Corbet, 1972). Their principal characters have been described by Lowe (1959) and Peters (1961) and again by Thys (1970). Some of the differences between *Coptodon* and *Sarotherodon* given by Thys do not distinguish all species of *Tilapia* (or *Coptodon*) from *Sarotherodon*, and even if one selects the most reliable, exceptions must be admitted. I would prefer to postpone my full definitions to a publication containing all the evidence in the form of specific descriptions, but in the hope of avoiding confusion I give what appear to be the most generally verified distinctions.

Tilapia

1. Gill-rakers 7–16 on the lower part of the first arch, more than 12 in only the three species of subgen. *Pelmatolapia* Thys.

2. Median length of lower pharyngeal bone 21·5–28·5% length of head (rarely up to 30·5 in *T. rendalli*).

3. Pharyngeal blade/median length of toothed area 0·3–0·75 (0·5–1·0 in *T. mariae*).

4. Mesethmoid meeting vomer in all except one species (*T. rendalli*) and some individuals of *T. dageti*, *T. guineensis*, *T. discolor*, and *T. zillii* (fig. 13).

5. Substrate spawners and guarders of the brood.

Sarotherodon

1. Gill-rakers on lower part of first arch 10–28, less than 13 in only three species.
2. Median length of lower pharyngeal bone 27·5–43·5% length of head in adult.
3. Pharyngeal blade/median length of toothed area (0·4) 0·8–3·5.
4. Mesethmoid not meeting vomer (fig. 14).
5. Mouth-brooders.

Comments on the distinguishing characters

The species of *Sarotherodon* with fewer than 13 gill-rakers in some individuals are *S. franchettii*, *S. alcalicus* and *S. amphimelas*, all inhabiting specialized biotopes.

The median length of the pharyngeal bone (as % length of head) increases with size of fish, especially in *Sarotherodon*, and in the majority of species of this genus it is 30% or more in adults.   In a few the minimum length is below 30%, but (except in *S. percivali*) the maximum always exceeds 30%, even in such small species as *S. alcalicus* and *S. franchettii*.   Of the species that grow to a good size the lowest range (25·5–31·5%) is found in *S. aureus*, nearly approached by *S. pangani*.

The species of *Sarotherodon* that have the pharyngeal blade often a little shorter than the toothed area in adults are *S. niloticus*, *S. aureus*, *S. urolepis*, *S. placidus*, *S. andersoni* and the three species of the Pangani system.   The exceptionally short ratio of 0·4 occurs in *S. pangani girigan*, in which the toothed area is enlarged and the teeth are unusually coarse.   In this category too comes *S. steinbachi* of Barombi Mbo, in which although the whole bone is very long and the teeth fine and crowded the toothed area is enormously enlarged.
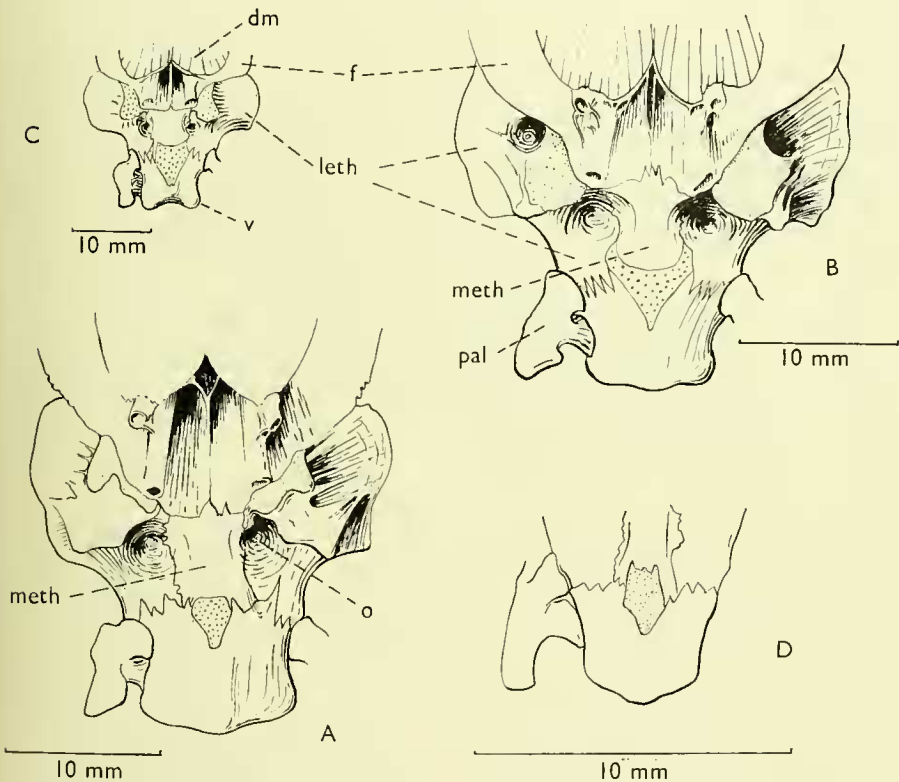
FIG. 13.   Ethmovomerine region in *Tilapia*.   A, *T. zillii* of SL 205 mm, Nile, B, *T. rendalli* of SL 200 mm, Lake Malawi, C, *T. dageti* of SL 170 mm, Gambia, D, *T. mariae* of SL 86 mm, Lake Barombi Kotto.   Cartilage dotted, *dm* dorsal muscles, *f* frontal, *leth* lateral ethmoid, *meth* mesethmoid, *o* olfactory foramen, *pal* head of palatine, *v* vomer.

The ethmo-vomerine relationship is illustrated in figs 13 and 14. The vomer surrounds the rostral end of the ethmoid cartilage and laterally makes a sutural union with the lateral ethmoid at the articular surface with the upper arm of the head of the palatine. In most cichlids (and other Perciformes) the mesethmoid ossification meets the vomer dorsally between these two points, forming a complete or nearly complete bony roof for the ethmoid cartilage. This is true of *Pelmato-chromis*, *Chromidotilapia* and the genera of the *Haplochromis*-group and also of *Tristramella* and most species of *Tilapia*, in which there is a small area of cartilage left free between right and left ethmo-vomerine sutures (fig. 13). But in *T. rendalli* (3 specimens tested) the anterior edge of the mesethmoid is rounded and free from the vomer. It was the contrast between *T. rendalli* on the one hand and *T. zillii* and *T. busumana* on the other that led Regan (1920) to recognize the subgenus *Coptodon* for *T. zillii* and *T. busumana*. Regan did not then know that the ethmo-vomerine sutures characterize also the type species of *Tilapia*, *T. sparrmanii* A. Smith.

We do not now consider it possible to separate *T. zillii* and *T. rendalli* sub-generically. Although the ethmo-vomerine union cannot be used as an absolutely diagnostic feature of *Tilapia*, its opposite, the freedom of these bones from each other, appears to be a constant feature of *Sarotherodon*, verified by me in at least one specimen each of fourteen species. *Sarotherodon* is specialized in this respect as also in its dentition, especially the pharyngeal, and in its reproductive arrangements.

One may suggest a possible functional explanation for the failure of the mesethmoid to meet the vomer in *Sarotherodon*. These predominantly microphagous species are characterized by a very broad head, providing a long and broad bucco-pharynx for the passage of large quantities of food-laden water. At the same time the stresses and strains on the jaw apparatus are far less than they would be in a predator, so that the fish can afford to broaden its ethmoid region without strengthening it with additional bone. It is the cartilage that is enlarged and in enlarging it appears to have separated the mesethmoid from the influence of the upper wings of
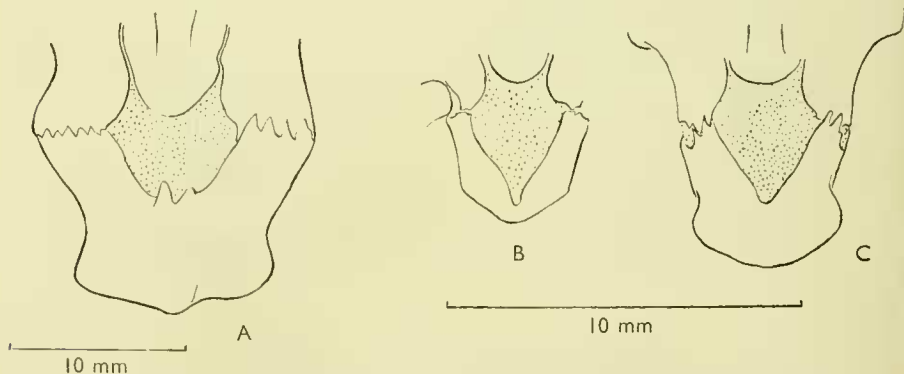

FIG. 14. Ethmovomerine region in *Sarotherodon* and *Stomatepia*. A, *Sarotherodon shiranus*, B, *Stomatepia mongo* and C, *St. pindu*. Cartilage dotted.

the vomer. A specimen of *Tilapia dageti* (fig. 13C) in which a tongue of the mesethmoid bone meets the vomer on one side gives a distinct impression of one bone influencing the other on the right side, whereas the rounded edge of the mesethmoid in *T. rendalli* (fig. 13B) and *Sarotherodon* (fig. 14A) looks like a bone developing freely from its own centre of ossification.

That the free ethmoid is not a necessary concomitant of a broad head is shown for instance by the South American *Cichlasoma bimaculata* (Linnaeus) a species with a very broad head in which the ethmoid cartilage is completely roofed by bone. Its dental equipment suggests that it feeds on bottom-living arthropods.

If the free ethmoid of *Sarotherodon* has arisen as a result of a functional response, it seems to have become genetically established so that the process is not reversible. So it is retained in the algal-grazing *S. alcalicus* and in the predatory *Stomatepia* of Barombi Mbo (fig. 14B and C), although the latter have developed narrow heads, strong jaws and short guts while showing affinity to *Sarotherodon* in the gill-raker numbers, pharyngeal bones and large, presumably mouth-brooded eggs (see Trewavas, Green and Corbet, 1972).

The following is a list of the species in which the ethmo-vomerine relationship has been examined, one specimen of each except where numbers follow the name. $\frac{1}{2}$ signifies meeting on one side but not the other; such specimens appear in both lists. In addition, in one *T. dageti* and two *T. discolor*, listed among those with a free ethmoid, the ethmoid sends out a short tongue on one side that fails to meet the vomer. To both lists are added the species of Barombi Mbo believed to be derivatives respectively of *Tilapia* and *Sarotherodon*.

Mesethmoid meeting vomer

Tilapia sparrmanii A. Smith (3)	*T. guinasana* Trewavas
T. busumana (Günther)	*T. zillii* Gervais (9)
T. dageti Thys van den Audenaerde ($1\frac{1}{2}$)	*T. kottae* Lönnberg
T. guineensis (Bleeker) ($\frac{1}{2}$)	*T.(?)camerunensis* Lönnberg
T. joka Thys van den Audenaerde	*Pungu maclareni* (Trewavas) (2)
T. mariae Boulenger	*Tristramella simonis* (Günther)

Mesethmoid free from vomer

Tilapia rendalli Boulenger (3)	*T. dageti* Thys ($3\frac{1}{2}$)
T. zillii Gervais (1)	*T. discolor* (Günther) (2)
T. guineensis (Bleeker) ($\frac{1}{2}$)	*Sarotherodon melanotheron* Rüppell (2)
S. galilaeus (Linnaeus)	*S. aureus* (Steindachner)
S. niloticus (Linnaeus)	*S. caroli* (Holly)
S. linnellii (Lönnberg)	*S. steinbachi* (Trewavas)
S. lohbergeri (Holly)	*S. percivali* (Boulenger)
S. spilurus (Günther)	*S. shiranus* (Boulenger)
S. amphimelas (Hilgendorf)	*S. alcalicus grahami* (Boulenger)
S. hunteri (Günther)	
Stomatepia mariae (Holly)	*Stomatepia pindu* Trewavas
Stomatepia mongo Trewavas	*Myaka myaka* Trewavas (2)
Konia eisentrauti (Trewavas)	*Konia dikume* Trewavas

The reproductive and parental behaviour patterns divide the genera quite sharply, in spite of much evidence that the mouth-brooders have descended from substrate-spawners; and the two patterns carry with them contrasting structural and developmental features that have been admirably analysed for the species known to them by Baerends & Baerends van Roon (1950), Lowe (1959), Peters (1961), Kraft & Peters (1963), Peters (1965), Fishelson (1966), Heinrich (1967) and others. On the one hand the mouth-brooders exhibit certain vestigial features that can only be interpreted as evidence of substrate-spawning ancestry—vestigial adhesive organs in the embryo, sparse adhesive threads on the egg surface in *S. galilaeus* and *S. melanotheron*. On the other hand certain parallel developments with *Sarotherodon* occur within *Tilapia*, of which the freedom of the ethmoid from the vomer in *T. rendalli*, though not connected with reproduction, is perhaps the most indicative of the close phyletic relationship of *Tilapia* with *Sarotherodon*. Without this the question might remain open as to whether the substrate-spawning ancestors of *Sarotherodon* were indeed *Tilapia* and not some other genus from which *Tilapia* and *Sarotherodon* might independently have developed the structural adaptations to a herbivorous diet.

Irvine & Trewavas (in Irvine, 1947) and Thys (1970) have suggested, from the presence of eggs or young in the mouths of 4 of a total of 23 mature males of *Tilapia discolor* examined, that a primitive mouth brooding may be practised by this species. Examination of two of these eggs by the electron scanning microscope showed the presence of sparse filaments on the surface, resembling those of *Sarotherodon galilaeus* rather than the dense filaments of *T. tholloni* figured by Kraft & Peters (1963). Before this is classified as parallelism with *Sarotherodon* more evidence is needed, even to prove that they were the eggs of the same species.   Their size-range (long diam. 2·6–3·2 mm) reaches that of known mouth-brooded eggs of *S. multifasciatus* (3·2 mm) of the same locality, Lake Bosumtwi. It need not be surprising to find mouth-brooding independently developed in *Tilapia* and *Sarotherodon*.   The species of *Tristramella*, closely related to *Tilapia*, are mouth-brooders (Ben-Tuvia, 1959) as well as others not so close.

A similar report by Pellegrin (1907a and b) concerning a '*Tilapia melanopleura*' of the Ogowe system with larvae in the mouth has generally been ascribed to the habit, well known in species of *Tilapia* (as well as other cichlid substrate-spawners) of transporting embryos from one pit to another.   This is less likely to be the explanation in the case of *T. discolor*, not only on account of the structure of the egg surface, but because the transpo tation usually occurs after hatching, when the adhesive egg-shells remain attached to the substratum.

Chardon & Vanderwalle (1971), in a study of the head of *T. discolor* and two other species of *Tilapia* and two of *Sarotherodon*, found that *T. discolor* shared with the other two *Tilapia* species certain differences from the two *Sarotherodon* and that such specific (or individual?) differences as he found between the *Tilapia* species had no bearing on the function of mouth-brooding.

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